THE PHYLOGENETIC ORIGIN OF JAWS IN VERTEBRATES: DEVELOPMENTAL PLASTICITY AND HETEROCHRONY

JOHN A. LONG
Natural History Museum of Los Angeles County
900 Exposition Boulevard, Los Angeles, California 90007
jlong@nhm.org

BRIAN K. HALL
Department of Biology
Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1

KENNETH J. MCNAMARA
Department of Earth Sciences
University of Cambridge, Downing Street, Cambridge CB2 3EQ, United Kingdom

AND MOYA M. SMITH
MRC Centre for Developmental Neurobiology
Kings College London, London Bridge, EC19 RT, United Kingdom

ABSTRACT

The bearing that agnathans have on the origin of jawed vertebrates is one of the great unsolved problems in vertebrate phylogeny. Here we propose a mechanism for the evolution of jaws in vertebrates based on a combination of evidence from the fossil record and from experimental developmental biology. In chick embryos, osteogenesis can be evoked experimentally from scleral mesenchyme by the same mandibular epithelium that evokes osteogenesis in the jaws. Sclerotic bones appeared before jaws in vertebrate phylogeny and scleral ossicles and jaw skeletons are linked by shared developmental processes. As only one group of fossil agnathans—the Osteostraci—has ossified sclerotic bones, they alone possessed the inherent developmental potential to develop bone in the lower jaws and are also considered the most probable sister taxon to gnathostomes.

Introduction

Nineteenth-century anatomists recognized that, based on embryonic development, innervation and vascular patterns, vertebrate jaws were the serial homologues of the skeletal branchial arches posterior to them (Gegenbaur, 1872). However, the skeletal support for the gill arches in living agnathans and gnathostomes are positioned differently (lateral in the former and medial in the latter) and so have been considered non-homologous (Goodrich, 1930; Schaeffer and Thomson, 1980). Mallatt (1984, 1996) suggested that an ancestral pregnathostome fish had two sets of branchial skeletal supports, one medial and one lateral, with the medial set being the current situation in all gnathostomes, while the lateral set is seen in living agnathans. Janvier (1996a) proposed that the lateral gill-arch cartilages are primitive for all vertebrates as the only set. Recent work by Kimmel et al. (2001) on neural crest ectomesenchyme in the zebrafish *Danio rerio* supports the notion that the lateral set of gill-arch structures comprise the gill arches in gnathostomes, and that, consequently, there is no barrier to the hypothesis that jaw cartilages arose from such gill-arch support cartilages.

A review of gnathostome origins by Forey and Janvier (1993) stated that "the way in which jaws develop remains unknown." On the basis of new paleontological data others have challenged the canonical view that jaws evolved from modification of the anteriormost branchial arches (Maisey, 1986). A review by Smith and Coates (2000) has emphasized the difficulties of accepting this classic segmentalist theory, of repetition of similar branchial arches, either on the basis of the phylogenetic changes proposed from the paleontological data, or from the developmental data. Janvier (1998) has compared succinctly the currently accepted theory with an alternative model, namely the conversion of skeletal structures supporting the velar feeding apparatus in the living agnathan lampreys, to the lower jaw cartilage of gnathostomes. This velar apparatus is quite anterior and medial

to the branchial basket, and supplied by the same nerves and homologous muscles as the jaws of gnathostomes. Shigeru Kuratani and his colleagues (Kuratani et al., 1999, 2001; Kuratani, 2003a, 2003b, 2004) showed that the lips of lampreys are derived from non-homologous embryonic components (mesoderm derived cartilage). With respect to crest derived cartilage of gnathostome jaws, the timing of neural crest emigration for the mandibular stream, some of which contributes to the cartilages, is identical in lampreys and gnathostomes. It appears to us that cartilaginous and jointed jaws could evolve from the velar ectomesenchymal condensations as either or both medial and lateral parts (Johnels, 1948), as Janvier (1996a, 1996b) proposed, and not by co-option of those of the more caudal branchiomeric arches. The addition of dermal bone for attachment of feeding elements to an articulated joint is another, as yet unrecognized, step and one we here consider to have occurred through developmental plasticity and heterochrony. It has become apparent that the evolution of jaws is not an example of co-option of one structure adapted for one function to take over another, i.e., from respiration to feeding (Smith and Coates, 2000). Equally, it is not an example of a parallel co-option of molecular patterning mechanisms used for anteroposterior positional information in the hindbrain to patterning the branchial arches, as suggested by Raff (1996). Mandibular arch with Hox-negative mandibular arch patterning appears to be separate from patterning of the gill arches (Graham, 2001; Graham and Smith, 2001), also the mandibular arches derive the bulk of their neural crest mesenchyme cells from the cephalic region (a small contribution from the midbrain with most rostral hindbrain). Kuratani (2003) postulated that the evolution of the vertebrate jaw developed as a change in developmental program for the specification of crest cells. All this raises important unanswered questions, such as, how the upper and lower jaws are linked in their development and evolution, and whether other developmental modules are part of this developmental matrix. Once dissociated from the development and evolution of gill arches, the concept that part of the anterior visceral skeleton including an osteogenic module, articulated with part of the rostral chondrocranium, may contribute to the developmental process forming jaws, becomes a possibility.

Phylogenetic Relationships

Two different pieces of evidence support agnathan thelodonts as a group sharing significant characters with gnathostomes; one, on the basis of stomachs preserved in the fork-tailed thelodonts (Wilson and Caldwell, 1993, 1998), the other on the evidence that branchial denticle whorls are present in one thelodont, *Loganellia scotica* (Van der Bruggen and Janvier, 1993) and in sharks. This has been supported by further studies comparing the arrangement of these branchial denticles with those of the early shark, *Akmonistion* (Smith and Coates, 2000, 2001; previously cited as *Stethacanthus* sp. (Coates and Sequiera, 2001)). The proposal made by Smith and Coates is that these could be an early example of oropharyngeal denticles in an agnathan able to be transformed through evolution to tooth whorls, inferred to be a primitive character of gnathostome vertebrates. It is proposed that these denticle groups exhibit a prepattern for the dentition as it evolved onto the jaw margins (Smith and Coates, 1998, 2000). Although thelodonts are probably a paraphyletic group with respect to more advanced pregnathostomes and gnathostomes (Janvier, 1996b), thelodonts may also include sub-adult osteostracans (of which juveniles are unknown). This could provide an explanation for the apparent absence of teeth or specialized oropharyngeal denticles in the closest sister-group to jawed vertebrates, the osteostraeans. Clearly, there is a problem here with (secondary?) absence of toothlike denticles in those groups which may include incipient stages in early jaw evolution. However, a cladistic analysis (Donoghue et al., 2000) proposes thelodonts as a monophyletic group, as opposed to the paraphyletic group proposed by Janvier (1981, 1996b). However, we note that Donoghue et al. did not test for monophyly of thelodonts.

Other phylogenetic analyses (Janvier, 1981, 1984, 1985; Forey, 1984; Forey and Janvier, 1993) support the view that the Osteostraci share more synapomorphies with gnathostomes than with any other agnathan group. These analyses were done before the fork-tailed thelodonts were recognized as a group. Numerous morphological characters link (toothless) osteostracan agnathans to placoderms and crown-group gnathostomes (Forey and Janvier, 1993; Janvier, 1996b), and this robust arrangement cannot be rejected easily. The only systematically argued alternative, which places thelodonts *sensu lato* as the immediate gnathostome sister-group (Wilson and Caldwell, 1998) has much lower resolution and uses a smaller data set.

Smith and Coates (1998, 2000, 2001) accept the fact that no satisfactory explanation of this apparently edentate stretch of gnathostome phylogeny has yet been presented. The extinct agnathan groups Galeaspida and Pituriaspida (Young, 1991) are also potential alternative sister taxa to the Gnathostomata, but incomplete data on the jaws and branchial skeleton preclude discussion here. Both Pituriaspida and Osteostraci probably had paired pectoral fins (assumed to be present in Pituriaspida) due to the large pectoral fenestra in their dermal armour (Young, 1991). Similarly, Osteostraci have perichondral bone developed in the neurocranium (a feature shared with gnathostomes), although little is known of the structure of the tail and pectoral fin (if present) in this group. It should be noted that the stated absence of perichondral bone in Galespida (Wang et al., 2005) has challenged previous statements that it is present in the neurocranium and is used to support their position close to Gnathostomata (Young, 1991). While the paleontological data suggests that several of these groups may be sister-groups to the Gnathostomata, resolution of this problem using cladistic methodologies is equivocal; character states require polarity which in some cases cannot be determined without arbitrary character weighting, or more complete anatomical data from new fossil discoveries.

Developmental Processes

There is a developmental link between those mechanisms integral to initiation of the bony scleral ring of the eyes (Figure 1) to that of the cartilage and bone of the jaws, Meckel's cartilage, and dermal membrane bones (Hall, 1981, 2005). All three skeletal components develop from neural crest-derived mesenchyme dependent on, and sequential to, inductive interactions with embryonic epithelia. Membrane bones of the lower jaw arise following interaction with mandibular epithelium. Scleral bones in birds (we do not know the inductive signals in reptiles or fish) arise following induction from specialized epithelial papillae overlying the eye (Hall, 1981, 2005; Pinto and Hall, 1991).

As an alternative to this source of the signal, osteogenesis can be evoked from scleral mesenchyme by mandibular epithelium. In experimental studies of chick embryos, scleral mesenchyme will develop into sclerotic bones of the eye following contact with mandibular epithelium, i.e., the bones are recognizably scleral ossicle. The epithelium provides a signal that is sufficient to
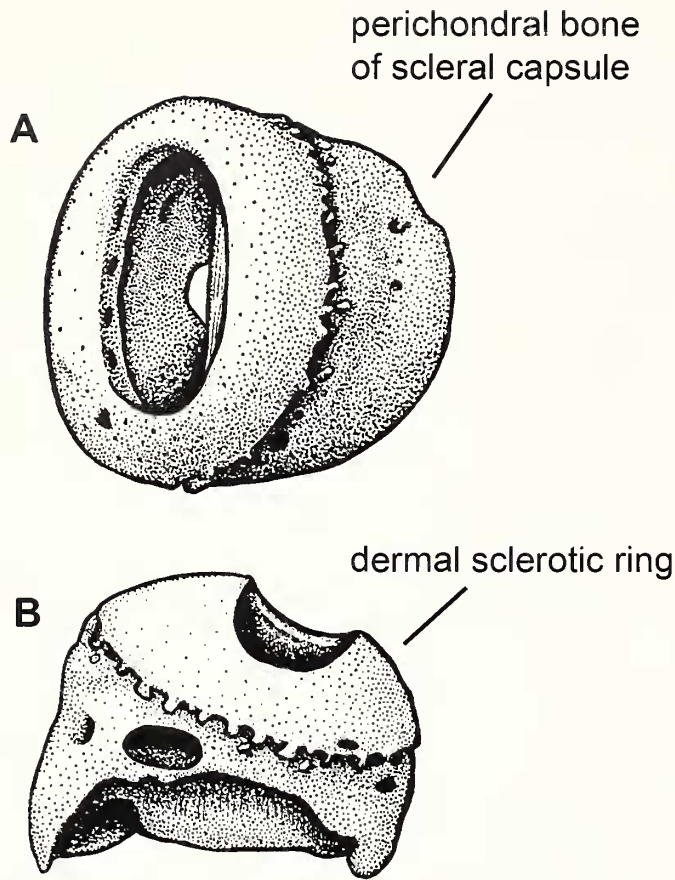
perichondral bone
of scleral capsule

dermal sclerotic ring

Figure 1. Fossilized sclerotic ring from the osteostracan *Tremataspis mammillata* Patten, after Janvier (1985).

initiate differentiation, but morphogenesis is controlled by the mesenchyme (Hall, 1981, 1982, 1989). It follows from these observations that the formation of lower jaw bones, at least in chick embryos—the one taxon for which experimental evidence is available—uses the same class of inductive mechanisms as do scleral bones. This is a putative, shared, homologous developmental mechanism (Hall, 1995, 2003) providing a link between developmental mechanisms underlying scleral ossicles of the eye and those that initiate chondrogenesis and osteogenesis in the jaws.

We suggest that evolutionary origin of the lower jaws in the first fishes may have been developmentally interconnected with the origins of sclerotic ring ossification. The scenario would be:

• neural crest cells migrate to surround the eye in a jawless vertebrate;

• neural crest cells migrate further ventrally and laterally as the primordia of the mandibular arch develop en route to jawed vertebrates;

• either inductively active epithelium migrated with neural crest cells as is known to occur in extant gnathostomes (Couly and Le Douarin, 1990); and/or

• mandibular arch neural crest cells interacted with adjacent epithelium to elicit inductive signaling (see Hall, 1992, for such a mechanism);

• bone was induced in the first lower jaws using the same developmental mechanism as evokes scleral bones, i.e., the

evolutionary origin of the jaw skeleton is developmentally linked to initial ossification around the eyes.

Further, Couly et al. (2002) revealed that the interaction between the head ectoderm and oral endoderm leads to the patterning of the jaw cartilages in the chick embryo.

Studies from both heterochrony and paleontology support this scenario.

Heterochronic Processes

The role of heterochrony in the appearance of major evolutionary novelties has long been recognized. McKinney and McNamara (1991) suggested that heterochronic processes involving changes to the timing of onset of initiation and growth of structures (predisplacement and postdisplacement) at very early developmental stages may have played a role in the evolution of some higher taxa, a view reinforced by Richardson et al. (1997) and Richardson (1999).

Hall (1984) has demonstrated how the timing of production of Meckel's cartilage varies between classes of vertebrates. It forms earliest in development in birds, later in amphibians and cyclostomes, and even later still in mammals. Phylogenetically this can be interpreted as peramorphic predisplacement in birds, relative to amphibians and cyclostomes, but paedomorphic postdisplacement in mammals (see Hall, 2000). The analogy between this and the appearance of jaws and sclerotic rings in fishes in evolution is through a similar inductive tissue interaction. If both scleral and mandibular mesenchyme can form bone in response to mandibular oral epithelium in birds, and assuming similar tissue interactions in other taxa, then the timing of jaw initiation is likely to be earlier in osteostracans than in jawless fishes, such as cyclostomes. In heterochronic terms (McKinney and McNamara, 1991) predisplacement in the timing of migration of the neural crest cells may have been a critical factor in triggering bone formations in fishes.

MacDonald and Hall (2001) demonstrated that the timing of the epithelial-mesenchymal interactions responsible for the production of Meckel's cartilage varies between three inbred strains of mice, and that timing of the interactions correlates with timing of condensation of the cells that give rise to Meckel's cartilage. The significance of this study is threefold:

1. providing an experimental demonstration that heterochrony is an evolutionary mechanism;

2. demonstrating that timing changes can occur between closely related taxa;

3. demonstrating that such timing changes can occur in the relatively short number of generations required to establish the inbred lines.

Molecular studies indicate the classes of genes that are likely to be responsible for such heterochronic changes; the most likely candidates are *Bmp-2* and *-4*, *Msx-1*, and *Fgf-4* and *-8* (Barlow and Francis-West, 1997; Chen et al., 2000; Ferguson et al., 2000; MacDonald and Hall, 2001; Hall, 2005).

We would expect onset of ossification of mandibular bones to be controlled similarly. Indeed, recent studies on teleost fish are consistent with teleost scleral ossicles having a closer relationship to scleral cartilage than to the scleral ossicles of other vertebrate groups, to the point that teleost ossicles may not be homologous with scleral ossicles in birds but with scleral cartilage; for example, fish ossicles arising in scleral cartilage, and avian ossicles as

separate dermal ossifications (Franz-Odendall and Hall, 2006). If this was true for the earliest agnathans, i.e., if their scleral ossicles arose in relation to cartilage, then the link we propose between jaw and scleral skeletons becomes even stronger, especially as scleral cartilages in reptiles and birds are initiated following an inductive interaction between mesenchyme and pigmented retinal epithelium (Pinto and Hall, 1991; Hall, 2005).

Fyfe and Hall (1981) and Hall (1981) discuss mutants, such as scaleless (sc) that prevent epithelial papillae formation, and thus inhibit cell condensations and scleral bone formation. McAleese and Sawyer (1982) showed that because the scaleless gene is first expressed in the ectoderm and later in the mesenchyme, combining embryonic sc/sc ectoderm with +/+ mesenchyme of the same age results in a scaleless phenotype. However, recombining sc/sc ectoderm with mesenchyme from older embryos results in a scaled phenotype being produced. Thus, the timing of gene expression is critical to papilla formation. Consequently, skeletal elements that arise following epithelial-mesenchymal interactions (Meckel's cartilage, scleral, and mandibular bones; see previous paragraph) can be interpreted as occurring by pre- or postdisplacement of the time of expression of genes expressed in inductively active epithelia.

Paleontological Data

The presence of ossified sclerotic bones in fossil agnathan fishes has been demonstrated only in one group—the Osteostraci (e.g., Janvier, 1985, fig. 1). Osteostracans have been proposed as the most likely sister-group to gnathostomes; they share the presence of paired pectoral fins, open endolymphatic ducts, dermal bone with cells, and an epicercal tail with modified scale cover (Janvier, 1981, 1984, 1985; Forey, 1984; Forey and Janvier, 1993).

Maisey (1986, 1988) proposed a close relationship between anaspids and gnathostomes based on six characters. Some of these are shared or of uncertain distribution. However, stronger more reliable characters uniting gnathostomes with osteostracans have been proposed by more recent workers. The presence of circumorbital bones in anaspids is not seen to be homologous with the bony sclerotic plates seen in osteostracans and some basal gnathostomes as these are not as strongly interlocking as in sclerotic plates, nor do they share a well-ossified fundal surface to the ossified eye capsule, a feature seen on osteostracans and basal placoderms (Janvier, 1985; Long and Young, 1988).

Thelodonts, a group of fossil agnathans lacking armoured plates, have also been proposed as a possible closer relative to gnathostomes (Janvier, 1981; Wilson and Caldwell, 1998). However, based on many well-preserved specimens of *Phlebolepis* (Ritchie, 1968), *Turinia* (Turner, 1982), and the more recently described deep-bodied fork-tailed furcacaudiforms from Canada (Wilson and Caldwell, 1993, 1998), all of which have the orbital region of the head well-preserved, the sclerotic bones are clearly absent in thelodonts. Lack of this developmental potential to form dermal bones anywhere, including the sclera, may preclude the thelodonts from a position where they could transform into gnathostomes with bones in the jaws. This difficulty disappears, or at the very least is lessened, if agnathan scleral ossicles formed in association with scleral cartilage.

Sharks also lack bone (except in some specialized regions like the base of fin brushes, see Coates et al., 1998), but they always have jaws and teeth. As to the presence of scleral bones in basal chondrichthyans, the Devonian shark *Cladoselache* (Dean, 1909) and some other Cleveland Shale sharks (e.g., as in Williams, 1998), show enlarged dermal scales surrounding the orbit that
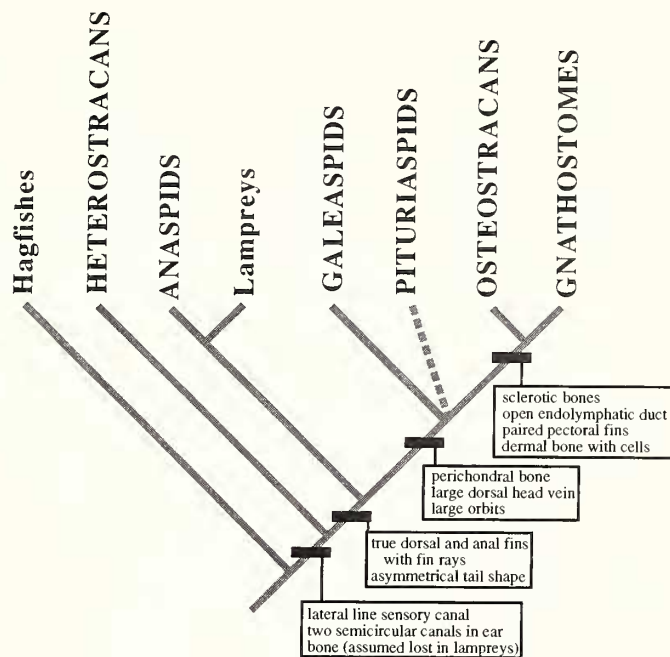

Figure 2. Preferred hypothesis of agnathan-gnathostome interrelationships based on the presence of scleral ossifications as inducers of jaw formation. Cladogram after Forey and Janvier (1984). Phylogenetic position of anaspids is unsure; they could alternatively be the sister-group to the node containing galeaspids and higher taxa (Janvier, 1975).

may be homologous to other gnathostome scleral bones or to circumorbital bones. In placoderms, dermal scleral bones are often highly ornamented, similar to their elaborate body scales (e.g., *Murrindalaspis*, Long and Young, 1988; Young, 2008) providing support for the hypothesis that scleral bones might well have originated primarily from enlargement of the dermal scales around the eyes. Similar rings of ornamented denticles surround the eye in Cleveland Shale "*Ctenacanthus*" (Williams, 1998).

Developmental Interpretation

On the basis of the developmental link between scleral and mandibular bone, we propose that osteostracans are the most likely sister-group to gnathostomes (Figure 2). In all the earliest gnathostome groups, such as acanthothoracid placoderms, even the fundal surface of the sclerotic capsule may be perichondrally ossified (Long and Young, 1988). This condition is also partially developed in osteostracans (Figure 1), with bone developing as a separate membranous ossification site as well as forming subperiosteally in the scleral cartilage capsule and, as discussed above, appears to be the condition in teleosts.

The evolution of jaws may not be simply related to the functional significance of the structures themselves (i.e., to support teeth and improve feeding ability), but is almost certainly constrained by developmental controls. These involve the timing of neural crest cell migration and changes in the timing of regulatory molecules within the developmental modules. Many early agnathans had well-developed oral plates lining the ventral border of the mouth, providing them with an effective feeding mechanism that operated in a manner similar to a lower jaw (Janvier, 1974, 1985). In some osteostracans, like *Tremataspis*, an
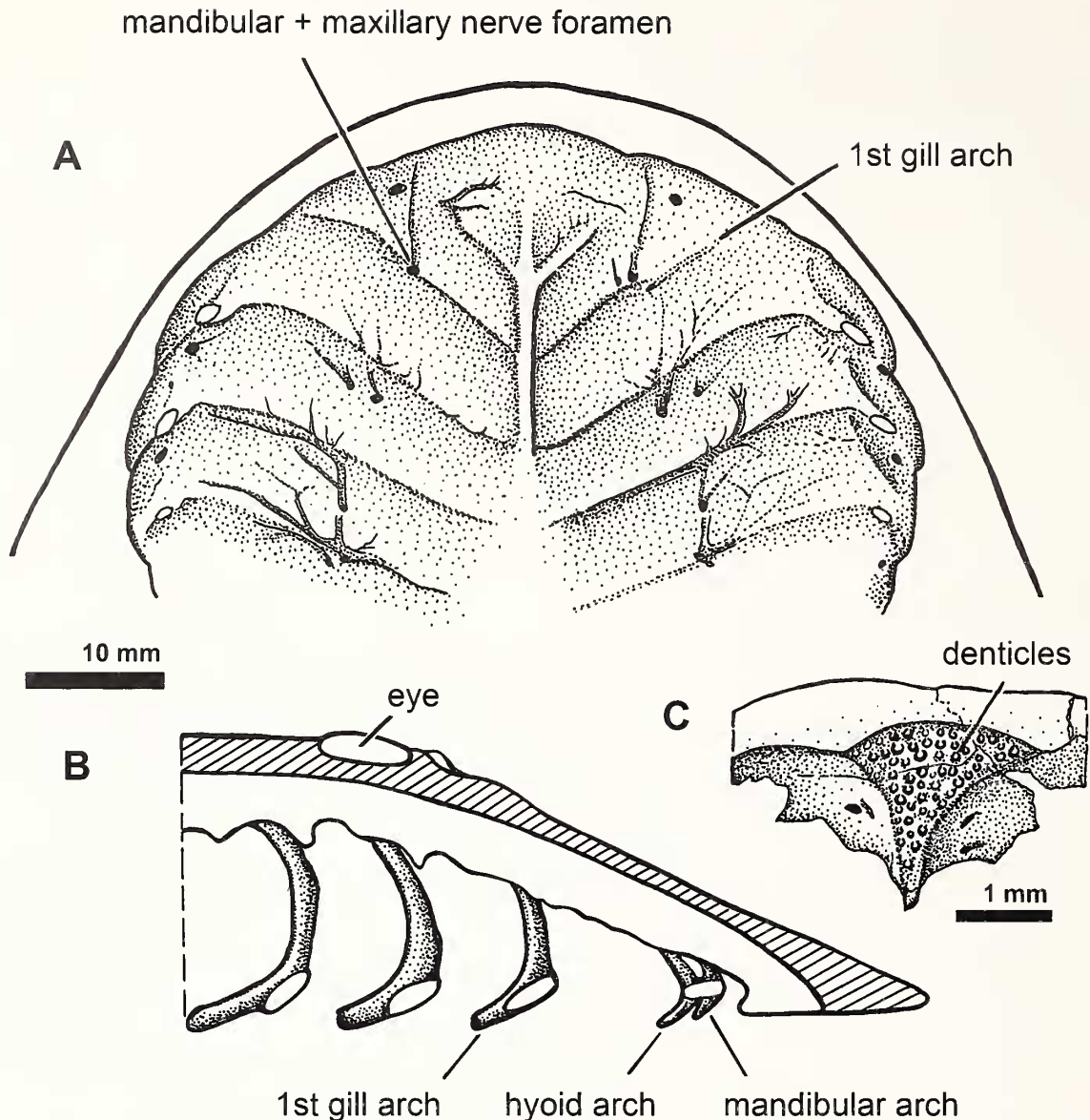
Figure 3. A, interpretation of orobranchial cavity in *Scolenaspis signata* (Wangsjo) from the Early Devonian of Spitzbergen with sagittal section (B) shown below, including attempted restoration of gill-arch elements. C, supraoral region of *Tremataspis mammillata* Patten from the Late Silurian of Estonia and Gotland, Sweden, showing intrabuccal denticles. After Janvier (1985).

anterior median lamina covered by denticles was situated just inside the roof of the mouth (Janvier, 1985, fig. 17; shown here in Figure 3C). This implies that a ventral structure may have acted against this surface for food reduction, possibly a denticle covered rasping organ, based on the lamprey model of the piston cartilage and "toothed" plate.

The inside visceral surface of the dorsal shields of osteostracans shows both the impressions of branchial pouches and grooves for the cranial nerves supplying the muscles that are presumed to operate skeletal cartilages of the branchial arches. Janvier (1996a) has reinterpreted these nerves from the first reconstruction of Stensiö (1958) to show that the mandibular and maxillary branches of the trigeminal are relatively much more anterior than previously thought. The foramen for the mandibular and maxillary nerves (V) is visible on the first branchial ridge in *Scolenaspis* and in several other osteostracans (Janvier, 1985).

Therefore, the branchial ridges of osteostracans situated close to the mouth margins may be homologous structures to the gnathostome jaws, and are topographically compatible with the quite anterior position of the velar cartilages in the lamprey. Moreover, the first two branchial pouches were situated well forward of the eyes (Figures 3A, 3B). Osteostracans presumably had cartilaginous gill-arch supports as shown by impressions of gill structures on the visceral surface of their shield. It is significant that these gill pouches are separate from the first two probable feeding arches. The developmental link between jaws and scleral formation is further emphasized by the fact that the ophthalmic nerve is also a branch of the fifth cranial nerve (as are the mandibular and maxillary nerves), serving to innervate the eyeball with small ciliary nerves.

Consequently, by small, but critical, changes to the timing of early developmental events, the evolution of the anterior

branchial arch elements to become primitive jaws did not necessitate large scale structural reorganization.

Acknowledgments

References

Barlow, A. J., and P. H. Francis-West. 1997. Ectopic application of recombinant BMP-2 and BMP-4 can change patterning of developing chick facial primordia. Development, 124:391–398.

Chen, Y., Y. Zhang, T. X. Jiang, A. J. Barlow, T. R. St. Armand, S. Heaney, P. H. Francis-West, C.-M. Chuong, and R. Mass. 2000. Conservation of early odontogenic signaling pathways in Aves. Proceedings of the National Academy of Sciences, U.S.A., 87:10040–10044.

Coates, M. I., I. J. Sansome, S. E. K. Sequeira, and M. M. Smith. 1998. Spines and tissues of ancient sharks. Nature, 396:729–730.

Coates, and Sequiera. 2001. A new stethacanthid chondrichthyan from the Lower Carboniferous of Bearsden, Scotland. Journal of Vertebrate Paleontology, 21:438–459.

Couly, G., S. Creuzet, S. Bennaceur, C. Vincent, and N. M. Le Douarin. 2002. Interactions between Hox-negative cephalic neural crest cells and the foregut endoderm in patterning facial skeleton in the vertebrate head. Development, 129:1061–1073.

Couly, G., and N. M. Le Douarin. 1990. Head morphogenesis in embryonic avian chimaeras: evidence for a segmental pattern in the ectoderm corresponding to the neuromeres. Development, 108:543–558.

Dean, B. 1909. Studies on fossil fishes (sharks, chimaeroids and arthrodires). Memoirs of the American Museum of Natural History, 5:211–287.

Donoghue, P. C. J., P. L. Forey, and R. J. Aldridge. 2000. Conodont affinity and chordate phylogeny. Biological Reviews, 75:191–251.

Ferguson, C. A., A. S. Tucker, and P. T. Sharpe. 2000. Temporospatial cell interactions regulating mandibular and maxillary arch patterning. Development, 127:403–412.

Forey, P. L. 1984. Yet more reflection on agnathan-gnathostome relationships. Journal of Vertebrate Paleontology, 4:330–343.

Forey, P. L., and P. Janvier. 1993. Agnathans and the origin of jawed vertebrates. Nature, 361:129–134.

Franz-Odendall, T. A., and B. K. Hall. 2006. Skeletal elements within teleost eyes and a discussion of their homology. Journal of Morphology, 267:1326–1337.

Fyfe, D. M., and B. K. Hall. 1981. A scanning electron microscopic study of the developing epithelial scleral papillae in the eye of the chick embryo. Journal of Morphology, 167:201 p.

Gegenbaur, C. 1872. Untersuchungen zur vergleichenden Anatomie der Wirbelthiere. III. Das Kopfskelet der Selachier. Engelman, Leipzig. 316 p.

Goodrich, E. S. 1930. Studies on the structure and development of vertebrates. Dover, New York. 837 p.

Graham, A. 2001. The development and evolution of the pharyngeal arches. Journal of Anatomy, 199:133–141.

Graham, A., and A. Smith. 2001. Patterning the pharyngeal arches. BioEssays, 23:54–61.

Hall, B. K. 1981. Specificity in the differentiation and morphogenesis of neural crest derived scleral ossicles and of the epithelial scleral papillae in the eye of the embryonic chick. Journal of Embryology and Experimental Morphology, 66:175–190.

Hall, B. K. 1982. How is mandibular growth controlled during development and evolution? Journal of Craniofacial Genetics and Developmental Biology, 2:45–49.

Hall, B. K. 1984. Developmental processes underlying heterochrony as an evolutionary mechanism. Canadian Journal of Zoology, 62:1–7.

Hall, B. K. 1989. Morphogenesis of the skeleton: epithelial or mesenchymal control? p. 198–201. In H. Splechtna and H. Hilgers (eds.), Trends in Vertebrate Morphology. Proceedings of the 2nd International Symposium on Vertebrate Morphology, Vienna, 1986. Fortschritte der Zoologie, 35. Fischer-Verlag, Stuttgart.

Hall, B. K. 1992. Cell-cell interactions in craniofacial growth and development, p. 261–267. In Z. Davidovitch (ed.), The Biological Mechanisms of Tooth Movement and Craniofacial Adaptation. EBSCO Media, Birmingham.

Hall, B. K. 1995. Homology and embryonic development. Evolutionary Biology, 28:1–37.

Hall, B. K. 2000. The evolution of the neural crest in vertebrates, p. 14. In L. Olsson and C.-O. Jacobsen (eds.), Regulatory Processes in Development. Wenner-Gren International series, Volume 76. Portland Press, London.

Hall, B. K. 2003. Descent with modification: the unity underlying homology and homoplasy as seen through an analysis of development and evolution. Biological Reviews of the Cambridge Philosophical Society, 78:409–433.

Hall, B. K. 2005. Bones and Cartilage: Developmental and Evolutionary Skeletal Biology. Elsevier/Academic Press, London. 760 p.

Janvier, P. 1974. The structure of the naso-hypophysial complex and the mouth in fossil and extant cyclostomes, with remarks on amphiaspiforms. Zoologica Scripta, 3:193–200.

Janvier, P. 1975. Les yeux des cyclostomes fossils et le probleme de l'origines des Myxinoides. Acta Zoologica, 56:1–9.

Janvier, P. 1981. The phylogeny of the craniate, with particular reference to the significance of fossil agnathans. Journal of Vertebrate Paleontology, 1:121–171.

Janvier, P. 1984. The relationships of the Osteostraci and the Galeaspida. Journal of Vertebrate Paleontology, 4:344–358.

Janvier, P. 1985. Les cephalaspides du Spitsberg: anatomie, phylogenie et systematique des osteostraces siluro-devoniens; revision des osteostraces de la Formation de Wood Bay (Devonien inferieur du Spitsberg). Cahiers de Paleontologie, C.N.R.S. edit., Paris. 244 p.

Janvier, P. 1996a. Early Vertebrates. Oxford University Press, Oxford. 326 p.

Janvier, P. 1996b. The dawn of the vertebrates: characters versus common ascent in the rise of current vertebrate phylogenies. Palaeontology, 39:259–287.

Janvier, P. 1998. Les vertebres avant le Silurien. Geobios, 30:931–950.

Johnels, A. G. 1948. On the development and morphology of the skeleton of the head of Petromyzon. Acta Zoologica, 70:139–279.

Kimmel, C. B., C. T. Miller, and R. Keynes. 2001. Neural crest patterning and the evolution of the jaw. Journal of Anatomy, 199:105–119.

Kuratani, S. 2003a. Evolution of the vertebrate jaw: homology and developmental constraints. Paleontological Research, 7:89–102.

Kuratani, S. 2003b. Evolutionary developmental biology and vertebrate head segmentation: a perspective from developmental constraint. Theory in Biosciences, 122:230–251.

Kuratani, S. 2004. Evolution of the vertebrate jaw: comparative embryology and molecular developmental biology reveal the factors behind evolutionary novelty. Journal of Anatomy, 205:335–347.

Kuratani, S., N. Horigome, and S. Hirano. 1999. Developmental morphology of the cephalic mesoderm and re-evaluation of segmental theories of the vertebrate head: evidence from embryos of an agnathan vertebrate, *Lampetrajaponica*. Developmental Biology, 210:381–400.

Kuratani, S., Y. Nobusada, N. Horigome, and Y. Shigetani. 2001. Embryology of the lamprey and evolution of the vertebrate jaw: insights from molecular and developmental perspectives. Philosophical Transactions of the Royal Society B, 356:15–32.

Long, J. A., and G. C. Young. 1988. Acanthothoracid remains from the Early Devonian of New South Wales, including a complete sclerotic capsule and pelvic girdle. Memoirs of the Australasian Association of Palaeontologists, 7:65–80.

MacDonald, M. E., and B. K. Hall. 2001. Altered timing of the extracellular-matrix-mediated epithelial-mesenchymal interaction that initiates mandibular skeletogenesis in three inbred strains of mice: development, heterochrony, and evolutionary change in morphology. Journal of Experimental Zoology, 291:258–273.

Maisey, J. 1986. Heads and tails: a chordate phylogeny. Cladistics, 2:201–256.

Maisey, J. 1988. Phylogeny of early vertebrate skeletal induction and ossification patterns. Evolutionary Biology, 22:1–36.

Mallatt, J. 1984. Early vertebrate evolution: pharyngeal structure and the origin of gnathostomes. Journal of Zoology London, 204:169–183.

Mallatt, J. 1996. Ventilation and the origin of jawed vertebrates: a new mouth. Zoological Journal of the Linnean Society, 117:329–404.

McAleese, S. R., and R. H. Sawyer. 1982. Avian scale development. IX. Scale formation by scaleless (sc/sc) epidermis under the influence of normal scale dermis. Developmental Biology, 89:493–502.

McKinney, M. L., and K. J. McNamara. 1991. Heterochrony: The Evolution of Ontogeny. Plenum Press, New York. 420 p.

Patterson, C. 1982. Morphological characters and homology, p. 21–74. *In* K. A. Joysey and A. E. Friday (eds.), Problems of Phylogenetic Reconstruction. Systematics Association Special Volume 21. Academic Press, London.

Pinto, C. B., and B. K. Hall. 1991. Towards an understanding of the epithelial requirement for osteogenesis in scleral mesenchyme of the embryonic chick. Journal of Experimental Zoology, 259:92–108.

Raff, R. A. 1996. The Shape of Life: Genes, Development, and the Evolution of Animal Form. University of Chicago Press, Chicago. 544 p.

Richardson, M. K. 1999. Vertebrate evolution: the developmental origins of adult variation. BioEssays, 21:604–613.

Richardson, M. K., J. Hanken, M. L. Gooneratne, C. Pieau, A. Raynaud, L. Selwood, and G. M. Wright. 1997. There is no highly conserved embryonic stages in the vertebrates: implications for current theories of evolution and development. Anatomy and Embryology, 196:91–106.

Ritchie, A. 1968. *Phlebolepis elegans* Pander, an Upper Silurian thelodont of Oesel, with remarks on the morphology of thelodonts, p. 81–88. *In* T. Orvig (ed.), Current Problems in Lower Vertebrate Phylogeny, Nobel Symposium, 4.

Schaeffer, B., and K. S. Thomson. 1980. Reflections on agnathan-gnathostome relationships, p. 19–33. *In* L. Jacobs (ed.), Aspects of vertebrate history. Essays in Honor of Edwin Harris Colbert. Museum of Northern Arizona Press, Flagstaff.

Smith, M. M., and M. I. Coates. 1998. Evolutionary origins of vertebrate dentitions: phylogenetic patterns and developmental evolution. European Journal of Oral Sciences, Supplement 1, 106:482–500.

Smith, M. M., and M. I. Coates. 2000. Evolutionary origins of teeth and jaws: developmental models and phylogenetic patterns, p. 133–151. *In* M. F. Teaford, M. M. Smith, and M. J. W. Ferguson (eds.), Development, Function and Evolution of Teeth. Cambridge University Press, Cambridge.

Smith, M. M., and M. I. Coates. 2001. The evolution of vertebrate dentitions: phylogenetic pattern and developmental models, p. 223–240. *In* P. E. Ahlberg (ed.), Major Events in Vertebrate Evolution. Taylor and Francis, London.

Stensiö, E. A. 1958. Les cyclostomes fossils ou ostracodermes, p. 173–425. *In* P. P. Grasse (ed.), Traite de Zoologie, 12(1). Masson, Paris.

Turner, S. 1982. A new articulated thelodont (Agnatha) from the Early Devonian of Britain. Palaeontology, 25:879–889.

Turner, S. 1991. Monophyly and interrelationships of the Thelodonti, p. 87–119. *In* M. M. Chang, Y. H. Liu, and G. R. Zhang (eds.), Early Vertebrates and Related Problems of Evolutionary Biology. Science Press, Beijing.

Van der Bruggen, W., and P. Janvier. 1993. Denticles in thelodonts. Nature, 364:107.

Wang, N.-Z., P. C. J. Donoghue, M. M. Smith, and I. J. Sansom. 2005. Histology of the galeaspid dermoskeleton and endoskeleton, and the origin and early evolution of the vertebrate cranial endoskeleton. Journal of Vertebrate Paleontology, 25:745–756.

Williams, M. E. 1998. A new specimen of *Tamiobatis vetustus* (Chondrichthyes, Ctenacanthoidea) from the Late Devonian Cleveland Shale of Ohio. Journal of Vertebrate Paleontology, 18:251–260.

Wilson, M. V. H., and M. W. Caldwell. 1993. New Silurian and Devonian fork-tailed 'thelodonts' are jawless vertebrates with stomachs and deep bodies. Nature, 361:442–444.

Wilson, M. V. H., and M. W. Caldwell. 1998. The Furcacaudiformes: a new order of jawless vertebrates with thelodont scales, based on articulated Silurian and Devonian fossils from northern Canada. Journal of Vertebrate Palaeontology, 18:10–29.

Wilson, M. V. H., and T. Marrs. 2004. Towards a phylogeny of the thelodonts, p. 95–108. *In* G. Arratia, R. Cloutier, and M. V. H. Wilson (eds.), Recent Advances in the Origin and Early Radiation of Vertebrates. Verlag Dr. Friedrich Pfeil, Munich.

Young, G. C. 1991. The first armoured agnathan vertebrates from the Devonian of Australia, p. 67–85. *In* M. M. Chang, Y. H. Liu, and G. R. Zhang (eds.), Early Vertebrates and Related Problems of Evolutionary Biology. Science Press, Beijing.

Young, G. C. 2008. Number and arrangement of extraocular muscles in primitive gnathostomes: evidence from extinct placoderm fishes. Biology Letters, 4:110–114.